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ABSTRACT

The native fan palms of the Baja California peninsula (Mexico) and neighboring southern California (USA) comprise two species each in *Washingtonia* and *Brahea*. While these are among the most familiar ornamental palms in the world, many features of their taxonomy, distribution, and environmental relationships remain unresolved. We utilized Google Earth Digital Globe imagery (and limited surveys by air and land) to develop the first map detailing the geographic distribution of palm populations in the Peninsular Range Province (PRP) and used these data to formulate new hypotheses on their biotic and abiotic relationships. We inventoried 15,216 populations covering an area of 8533 ha, containing an estimated 1.31 million trees. Tree populations estimated by manual tallies from Google Earth images closely matched direct counts published by previous workers. We documented significant extensions in the distributions of both *Washingtonia* species, as well as 66 hitherto unreported *W. robusta* oases in the Sierra La Asamblea. We also recorded thousands of upland populations of dwarf *B. armata*. Google Earth imagery shows that native fan palms are widespread in remote mountains of the entire peninsula, but in Baja California Sur *W. robusta* is mostly restricted to a few highly altered agricultural landscapes associated with extensive wetlands. It has long been assumed that the center of *W. robusta* distribution is in the tropical southern peninsula. Our observations suggest it may have been dispersed there by indigenous peoples before European contact, and its center of genetic diversity may instead lie in the Central Desert (ca. lat 28°–30°N).

RESUMEN

Las palmas de abanico nativas de la Península de Baja California (México) y las vecindades del sur de California (EUA), incluyen dos especies en cada uno de los géneros *Washingtonia* y *Brahea*. Aunque estas palmas son algunas de las plantas de ornato más familiares del mundo, muchos aspectos de su taxonomía, distribución y relaciones ambientales aún no se han resuelto. Utilizamos imágenes de Google Earth Digital Globe (y reconocimientos por aire y tierra) para desarrollar el primer mapa detallado de la distribución geográfica de poblaciones de palmas en la Provincia de la Cordillera Peninsular (PRP), y usamos esos datos para formular nuevas hipótesis sobre sus relaciones bióticas y abióticas. Registramos 15,216 poblaciones cubriendo un área de 8533 ha, con un total estimado de 1.31 millones de árboles. Estimaciones de poblaciones de palmas por conteo manual en imágenes de Google Earth dieron resultados similares a los conteos directos sobre terreno publicados por trabajadores previos. Registramos extensiones significativas en las distribuciones de ambas especies de *Washingtonia*, y descubrimos 66 poblaciones de *W. robusta* en los oasis de la Sierra de La Asamblea que no se habían reportado. También encontramos miles de poblaciones de individuos enanos de *B. armata*. Las imágenes de Google Earth demuestran que las palmas nativas tienen una amplia distribución en partes remotas de las montañas en toda la península, pero en Baja California Sur *W. robusta* se restringe generalmente a los paisajes agrícolas asociados a los humedales extensivos. Por mucho tiempo se ha considerado que el centro de distribución de *W. robusta* se encuentra en la península meridional. Nuestras observaciones sugieren que en esta región tropical, la especie fue dispersada por los indígenas antes del contacto europeo, y su centro de diversidad genética se encuentra en el Desierto Central (ca. lat 28°–30°N).

Key words: Arecaceae, Baja California, *Brahea*, dwarf form, Google Earth, oasis, Peninsular Range Province, remote sensing, species mapping, *Washingtonia*.

INTRODUCTION

The Peninsular Range Province (PRP)—the arid mountainous region of the Pacific coast from southern California (USA) to Cabo San Lucas, Baja California Sur (Mexico)—is the northwestern limit in the geographic range of the palm family (Arecaceae) in the Americas. The native fan palms of the PRP, which comprise two species each in *Washingtonia* and *Brahea*, are among the most widely cultivated ornamental palms in the world. Despite the economic importance of Californian fan palms, however, much remains unclear about the origin and localities of their type specimens, their taxonomy and geographic distributions, as well as other biotic and abiotic

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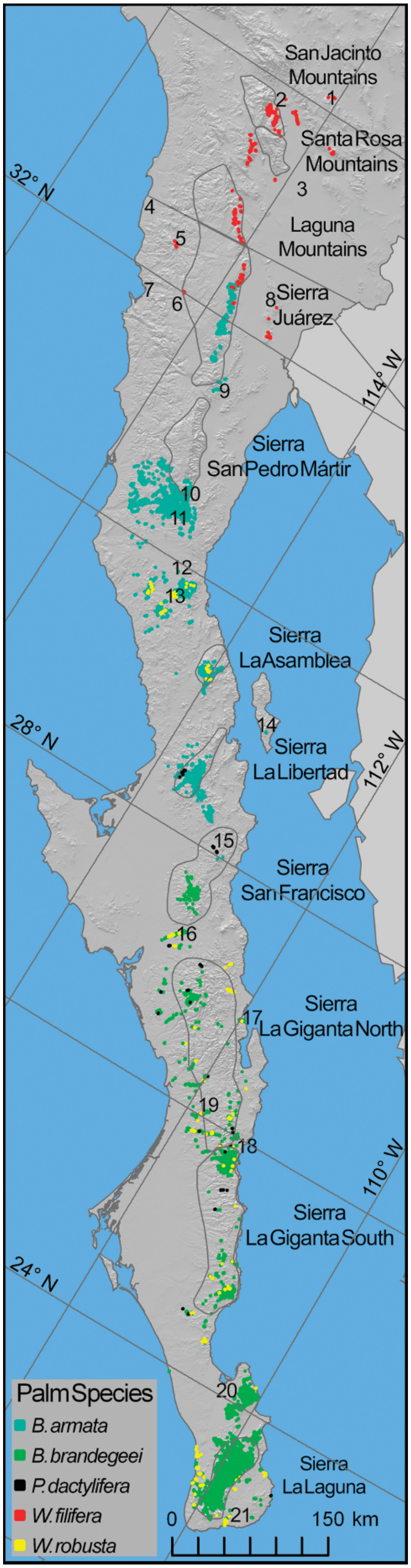

relationships (Ishihata and Murata 1971; Henderson et al. 1995; Turner et al. 1995; Felger and Joyal 1999; Felger et al. 2001).

The range of blue fan palm (*B. armata* S.Watson) extends from just south of the United States-Mexico border (Moran 1978) southward to just north of the state line of Baja California Sur in the central peninsula (Wiggins 1980; Franco-Vizcaíno et al. 2007) (Fig. 1). Brandegee fan palm (*B. brandegeei* (Purpus) H.E.Moore) extends from northern Baja California Sur to the cape region (Felger and Joyal 1999; Felger et al. 2001). Thus, the transition between the two species appears to be near lat 28°N, the political boundary between the two Mexican states of Baja California and Baja California Sur. The exact limits in the ranges of *B. armata* and *B. brandegeei* are unclear because of taxonomic uncertainties (Wiggins 1980; Minckley and Brown 1982; Hickman 1993; Henderson et al. 1995; Felger and Joyal 1999; Felger et al. 2001).

The taxonomy and distributional limits of *Washingtonia filifera* (Linden ex André) H.Wendl. ex de Bary, and *W. robusta* H.Wendl. are even more ambiguous. For example, a morphologically ''intermediate form'' was described in a population of cultivated *Washingtonia* spp. introduced into Japan in 1914 (Ishihata and Murata 1971). The northern species, *W. filifera* (California or desert fan palm), occurs mainly in southeastern California, northern Baja California, and western Arizona (Munz and Keck 1959; Wiggins 1980; Minckley and Brown 1982; Cornett 1985*b*; Hickman 1993; Schoenherr and Burk 2007). The southern species, *W. robusta* (Mexican fan palm or ''skyduster'', a form nearly emblematic of Hollywood and the movies), is widely distributed in Baja California Sur and locally in the northern Central Desert of Baja California, as well as across the Gulf of California near Guaymas, Sonora, at lat 27°N (Wiggins 1980; Minckley and Brown 1982; Felger and Joyal 1999; Felger et al. 2001).

Although *Washingtonia* spp. are more widely known and cultivated, trade in ''blue'' fan palms is also extensive because of their hardiness and unusual color. A fifth Californian fan palm, the elegant ornamental *Brahea edulis* H.Wendl. ex S.Watson, is endemic to Isla Guadalupe, a volcanic island located 200 nautical miles SW of Ensenada which is not part of the PRP.

The mapping of palms became possible on Google Earth™ with the recent addition of high-resolution Digital Globe

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Fig. 1. Distributions of native populations of *Washingtonia* and *Brahea* fan palms, and introduced date palm (*Phoenix dactylifera*) in the Peninsular Range Province (a zoomable version of this map may be viewed at: *http://ccb.ucr.edu/aliso.html*). The principal mountain ranges are outlined, and numbers show the locations of place names mentioned in the text. USA: (1) Twentynine Palms, (2) Palm Springs, (3) Salton Sea. Mexico: (4) Tijuana, (5) Valle de las Palmas, (6) Ojos Negros, (7) Ensenada, (8) Sierra Cucapah, (9) Arroyo Grande, (10) Arroyo El Berrendo, (11) Mesa Matomí, (12) El Mármol, (13) Cataviña-Santa Inés-Misión Santa María, (14) Isla Angel de la Guarda, (15) Misión Santa Gertrudis, (16) San Ignacio, (17) Loreto, (18) Mulegé, (19) San José Comondú, (20) La Paz, (21) Los Cabos. The Central Desert is the region between the southern Sierra San Pedro Mártir and the northern Sierra San Francisco (ca. lat 30–28°N).

imagery. The distribution of fan palms in the PRP has been broadly documented from botanical collections, field observations, and regional floras (Shreve 1951; Vogl and McHargue 1966; Moran 1978; Wiggins 1980; Minckley and Brown 1982; Cornett et al. 1986). For example, all known populations of *W. filifera* in southern California have long been mapped because of the palm's value as an ''indicator species'' for water (Cornett 1988). These early data, however, gave little indication of the actual numbers of palm groves or their distribution. Indeed, a relatively recent atlas of Sonoran Desert plants (Turner et al. 1995) shows a total of only 8 palm collection vouchers and 17 sightings for the entire peninsula.

We present the first high-resolution map of fan palm populations in the PRP, based on 15,216 polygons of palm populations, covering an area of 8533 ha, and use this database to develop new hypotheses on their environmental relationships. Understanding the complex interconnections between the geographic distribution of the PRP's four native fan palms and climate, terrain, bedrock, associated vegetation, and agencies of seed dispersal should help facilitate the future resolution of the taxonomy and evolutionary relationships of these poorly known, but economically important species.

METHODS

Geology and Climate of the Study Area

The PRP comprises the long and narrow Baja California peninsula and adjoining lands bordering the Salton Sea trough in southern California (Fig. 1). The region is a single mountainous unit of mostly granitic rocks that forms discontinuous ranges running parallel to the Gulf of California with intervening alluvial fans and plains. The crest often consists of broad plateaus that are bordered by intermittent, steep fault escarpments falling towards the gulf. The Pacific slope comprises gentle westward-dipping slopes that grade into alluvial plains. The ''spine'' of the PRP uniformly exceeds an elevation of 1500 m north of lat 30°, with summits reaching 3000 m. The peninsula to the south is generally below 800 m in elevation, with local summits exceeding 1400 m.

The formation of the Peninsular Range batholith (a very large intrusion of igneous rock) in the Cretaceous divided the peninsula's geologic history into three periods. This has resulted in three main types of soil parent materials: (1) pre-batholithic rocks characterized by mostly meta-sedimentary and meta-volcanic formations, (2) the ''granitic'' (granodiorite and tonalite) rocks of the batholith itself, and (3) post-batholithic volcanic rocks (basalt and pyroclastic materials) associated with tectonic rifting and opening of the Gulf of California (Gastil et al. 1975). The ongoing separation of the peninsular batholith from the adjoining North American continent has resulted in the opening of the Gulf since the Pliocene (5.3 million years ago [Mya]), and coincided with the uplift and westward tilting of the range since the Pleistocene boundary (1.8 Mya) (Gastil et al. 1975; Dickinson 1981). Classifications of geological formations throughout this article are based on Gastil et al. (1975), INEGI (1988), Todd (2004), and Morton and Miller (2006).

The Peninsular Range presents one of the most clearly defined Mediterranean-tropical (summer-dry vs. winter-dry) transitions in the world. The climate in the coastal plains and mountains from the Sierra San Pedro Mártir northward (lat 30°N) is Mediterranean with winter rain and summer drought. The lift of frontal storm air masses from North Pacific Ocean cyclones over continuous high terrain assures a reliable winter rainy season. South of the Sierra San Pedro Mártir, moist storm air masses yield little orographic precipitation due to the low elevation of the mountains.

High elevations of the PRP experience thunderstorms of the North American monsoon in summer. The heaviest summer rainfall occurs in the cape region, decreasing northward to the central peninsula, and increasing again in the high northern ranges. The southern peninsula is struck by east Pacific tropical cyclones about once a year near La Paz, decreasing to once per decade in southern California (Smith 1986). Average annual precipitation along the spine of the PRP varies from 40–70 cm north of the Sierra San Pedro Mártir, to 10–30 cm in the Central Desert, 30–40 cm in the Sierra La Giganta, and 70 cm in the Sierra La Laguna (Reyes-Coca et al. 1990).

Mediterranean vegetation of chaparral, oak woodland, and mountain conifer forest extend from southern California to the Sierra San Pedro Mártir (Minnich and Franco-Vizcaíno 1998). To the south, desert scrub assemblages extend from coast to coast across the spine of the peninsula at low elevations (Wiggins 1980; Minckley and Brown 1982). Tropical pine-oak woodland covers the Sierra La Laguna and adjoining ranges of the cape region (Maya et al. 1997).

Mapping of Palm Populations

The palms of the PRP were inventoried using high-resolution Digital Globe imagery of Google Earth (2005). Imagery was examined by graduated scaling, allowing for the observation of broad-scale patterns of vegetation and terrain at small scales, and near-ground identification of vegetation features. A measuring function was used for distance and slope, based on coordinate and elevation data.

Mature palms are readily mapped in arid regions due to their unusual morphology. Characteristic of most palms across the world, *Brahea* and *Washingtonia* palms have one unbranched bole with a single apical growing point and a canopy of leaves at the stem apex. A shag of dead fronds extends down the bole unless it is burned by fire or detached by flood or wind. On Google Earth imagery, palm canopies appear as near-perfect circles, with a central ''dimple'' due to shadowing near the meristem. With high sun angles, palm shadows appear as a single bole and circular leaf crown at the stem apex. *Brahea* fan palms have an azure blue color, but *B. brandegeei* is slightly greener than *B. armata*. *Washingtonia* crowns are yellow-green and can be easily distinguished from *Brahea* spp. where the two genera grow together (Fig. 2–3). The different species of *Brahea* and *Washingtonia* cannot be differentiated unequivocally, but they are not reported to grow together.

The interpretation of Google Earth imagery was conducted in two phases. In the first phase, palm oases were mapped by relying on the association of palms with riparian habitats (i.e., canyons and other wet sites) that were examined throughout the PRP. This step resulted in the mapping of ca. 80% of all oases. This approach of course is circular, because it is based on subjective and incomplete understanding of palm ecology. In the second phase, Google Earth imagery was scanned comprehensively in an ''X-Y'' format, including extensive

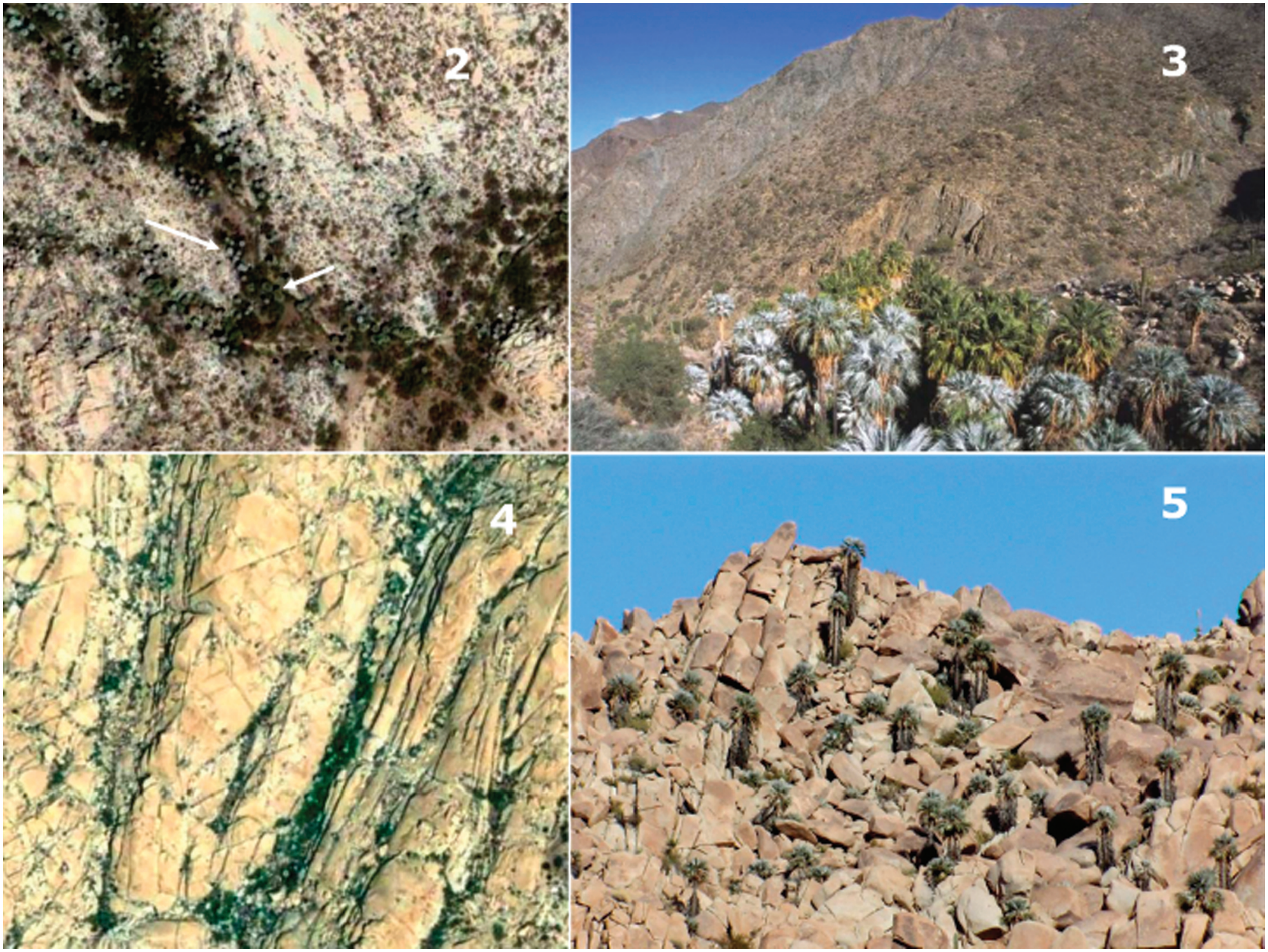

Fig. 2–5. Fan palm oases in the Baja California peninsula (Mexico).—2. Google Earth image of *Washingtonia robusta* (dark green, short arrow) along a moist watercourse and *Brahea armata* (bluish-gray, long arrow) on drier slopes above on a resistant granitic formation in the southeastern Sierra La Asamblea.—3. Oasis of *Washingtonia robusta* (green) and *Brahea armata* (grayish-blue) along a watercourse on the west slope of the Sierra La Asamblea (photo courtesy of K. Geraghty).—4. Google Earth image of dwarf *Brahea armata* on resistant granitic bedrock slopes at Cataviña.—5. Dwarf *Brahea armata* on granitic bedrock slopes in the Arroyo El Berrendo watershed, southern Sierra San Pedro Mártir (photo by EFV).

areas where no palms were found. This phase resulted in the discovery of the remaining mapped oases in this inventory.

To maximize the efficiency of scanning, imagery was examined at the smallest possible scale while maintaining resolution of palms, ca. 1500 m above-ground. When a population was suspected or encountered, Google Earth was scaled to ca. 600 m above-ground to confirm identification. Closer inspection was not possible due to pixelation. Although the examination of imagery is monoscopic, the tilt feature in Google Earth was used for three-dimensional viewing of terrain and rock substrate properties of individual palm populations. Limited resolution does not permit the use of the tilt function for 3-D viewing of palm morphology. Digital Globe imagery was unavailable at a few localities, including the southern Sierra Juárez, lands south of Cataviña, and portions of the Sierra La Libertad. In these areas, populations were mapped from older aerial photographs (1956; on file, Department of Earth Sciences, University of California, Riverside) and confirmed by low-altitude visual and photographic reconnaissance using a small aircraft. We also used land transport to conduct visual and photographic surveys of palms from the Sierra Juárez southward to the transitional zone between *Brahea* species in the southern Sierra La Libertad and the Sierra San Francisco.

The maps produced in this study were developed by digitizing directly onto Google Earth imagery, using the digitizing feature of the program. Polygons were mapped at ca. 600 m above-ground to maximize accuracy of boundaries. The integrity of digitizing was maintained with different landscape perspectives by changing the scaling and tilt of images. The palm database digitized on Google Earth was saved in the compressed version (kmz) of the keyhole markup language (kml) and placed into a compressed format. The file was subsequently saved in uncompressed (kml) format and converted to a standard GIS vector format, using ESRI ArcGIS Desktop 9.2 operating under an ArcInfo license (Environmental Systems Research Institute, Inc. 2005). Data were converted from the kml format to a feature classes ("shape") file for use in ArcGIS.

To estimate the total numbers of trees in the PRP, palms were counted manually in a random sample comprising ca. 1% of the mapped polygons. To verify the accuracy of palm counts in Google Earth images, we made a separate inventory of palms in 421 polygons in 16 palm canyons of southern California and northern Baja California in order to compare it with previously published in situ direct counts.

RESULTS

Little information has been available about the geographic distribution and number of palm populations in the PRP, although the presence of hundreds of fan palm oases was revealed by photointerpretation of aerial images of the southern (Maya et al. 1997) and northern peninsula (Minnich and Franco-Vizcaíno 1998). Mapping from Google Earth images now enables us to report the occurrence of 15,216 populations of fan palms covering an area of 8533 ha (Fig. 1, Table 1). These results, which are based on current interpretations of taxonomy and ranges of species (Moran 1978; Wiggins 1980; Felger and Joyal 1999; Felger et al. 2001), showed that *Washingtonia filifera* extends from southern California to the southern Sierra Juárez (ca. lat 31.4°), while *W. robusta* occurs locally from Cataviña to the Sierra La Asamblea (ca. lat 30° to 29°). *Brahea armata* ranges from just south of the United States-Mexico border to the southern Sierra La Libertad (ca. lat 28.25°), and *B. brandegeei* from the Sierra San Francisco (ca. lat 27.75°) to Cabo San Lucas. Hence, the transition between *Washingtonia* species appears to occur at ca. lat 30°N, and that between *Brahea* species at ca. lat 28°N. In Baja California Sur, *W. robusta* grows largely in major agricultural oases such as San Ignacio, Mulegé, and San José Comondú (Arriaga et al. 1997; Maya et al. 1997), with small populations occurring rarely in the Sierra La Giganta and the mountains of the cape region.

A random sample of 147 polygons gave an average density of 154 stems ha^{-1}, and an estimated total of 1.31×10^6 individuals of all four taxa in the PRP (Table 1). The size-frequency distribution of polygons was exponential with nearly 90% of populations <1 ha, and the largest at 72 ha. Populations are smallest in the north and disproportionately larger south of San Ignacio due to the presence of large agricultural oases.

Tree density and total numbers estimated in this study (Table 1) compare favorably with direct counts of palm numbers in all known oases in southern California (20,983 mature trees) recorded on the ground (Cornett et al. 1986). Moreover, correlation analysis revealed that tallies from Google Earth images closely matched previously published direct counts (Henderson 1971; Cornett et al. 1986) in 16 of the largest palm canyons in southern California and northern Baja California (Google Earth tally = 70.6 + 0.917 [direct count], r = 0.99; tallies in single canyons ranged from 178 to 4291 individuals). This result implies that, for each population tallied, some 71 trees were not discernible on the Google Earth imagery, and that in general populations were further underestimated by about 8% overall. Palms may be missed in such tallies because they are small, hidden from view under the canopy, or cannot be unambiguously differentiated from other features such as boulders or shrubs. The close correspondence with previously published records, however, suggests that populations in the northern PRP have been relatively stable since the counts were made 25–50 years ago.

A close look at the mapped polygons showed that palm populations generally form local colonies or elongate riparian galleries, with palms growing almost entirely in areas of supplemental water, at springs and seeps, and along water courses with intermittent surface water (see also Franco-Vizcaíno et al. 2007). High-elevation oases are dominated by *Brahea* spp., while *Washingtonia* spp. are most abundant in large oases at the base of the mountains (Fig. 1). *Washingtonia filifera* and *W. robusta* seldom grow above 1000 m elevation, while *B. armata* is found as high as 1400 m in the Sierras Juárez and San Pedro Mártir, and 1500 m in the Sierra La Libertad. *Brahea brandegeei* occurs as high as 1700 m in the Sierra La Laguna.

In southern California, several *W. filifera* oases grow on perched water tables along geologic faults, including the San Andreas fault near Palm Springs. From Palm Springs southward to the southern Sierra Juárez, most oases occur in arroyos along the arid eastern escarpment. *Brahea armata* joins *W. filifera* south of the U.S.-Mexico border, and the two species co-occur along the desert slopes of the Sierra Juárez

Table 1. Numbers and areas of mapped polygons, and estimated numbers of native and introduced palms,[a] in the various regions of the Peninsular Range Province.

Region/species	SCA	SJZ	SPM	CAT	ASB	SLB	SSF	SIG	NGI	SGI	CAP[b]	Total
POLYGONS (number):												
Wf	546	103										649
Ba-Wf		59										59
Ba		612	2645	1196	1464	1415	3					7335
Wr				47	25			1	1		1	75
Ba-Wr				54	41							95
Ba-Pd							1					1
Bb							179	27	247	1497	4758	6708
Bb-Wr								9	18	59	58	144
Bb-Wr-Pd								5	10	24	16	55
Bb-Pd								6	13	21	3	43
Wr-Pd								1				1
Pd						16	5	3	8	18	1	51
Total polygons	546	774	2645	1297	1530	1431	188	52	297	1619	4837	15,216
AREA (ha):[c]												
Wf	107	20										127
Ba-Wf		42										42
Ba		260	911	136	137	558	0					2002
Wr				21	2				0			23
Ba-Wr				30	6							36
Ba-Pd							0					0
Bb							74	267	96	331	4310	5078
Bb-Wr								27	116	80	129	352
Bb-Wr-Pd								33	260	435	98	826
Bb-Pd								11	12	17	0	40
Wr-Pd								0				0
Pd						1	4	0	1	1	0	7
Total area	107	322	911	187	145	559	79	338	485	864	4537	8533
Estimated number of trees (thousands)[d]	16.5	49.6	140	28.8	22.3	86.1	12.0	52.0	74.7	133	699	1314

[a] *Washingtonia filifera* (Wf), *Washingtonia robusta* (Wr), *Brahea armata* (Ba), *Brahea brandegeei* (Bb), and introduced *Phoenix dactylifera* (Pd). Classification of taxa was based on current interpretations of taxonomy and geographic ranges of species. Mountain ranges are arranged sequentially from N to S: SCA, southern California (USA). Mexico: SJZ, Sierra Juárez/Sierra Cucapah; SPM, Sierra San Pedro Mártir; CAT, Cataviña-Santa Inés-Misión Santa María; ASB, Sierra La Asamblea; SLB, Sierra La Libertad/Isla Angel de la Guarda; SSF, Sierra San Francisco; SIG, San Ignacio; NGI, northern Sierra La Giganta; SGI, southern Sierra La Giganta; CAP, cape region.

[b] Includes three beach oases with *Cocos nucifera*.

[c] Values < 1 ha are marked as "0".

[d] Calculated by multiplying regional area totals times mean density of palms (153.9 trees/ha $\pm$ 15.4 SE) determined by manual tallies in a sample of 147 polygons selected at random.

(Fig. 1). A 90-km gap of palms exists along the precipitous eastern escarpment of the northern Sierra San Pedro Mártir (elevational relief as much as 2500 m), but extensive monotypic stands of *B. armata* grow on its southern flank, and onto the western slope almost to the Pacific coast in a mixture of batholithic rocks, prebatholithic volcanics, and metamorphics.

The mountains near Cataviña have numerous oases of *B. armata* and *W. robusta* growing along arroyos scoured into batholithic and prebatholithic bedrock. A second line of oases occurs in a coastal range about 40 km from the Pacific Ocean. In the southern Sierra La Asamblea, extensive open woodlands of *B. armata* grow on a granitic formation in association with open chaparral. Dense stands of both *B. armata* and *W. robusta* descend in arroyos along the eastern escarpment (Fig. 1–2).

The southern Sierra La Libertad contains abundant *B. armata* oases in dissected Miocene basalt tablelands overlying granitic basement. Palms across the summit plateaus form open populations on volcanic caprock and on exposed granitic rock below the volcanic unit. Some oases on the volcanic summit plateau grow in "vernal pools" (shallow depressions) formed on the surfaces of Pliocene lava flows. A single grove of ca. 100 *B. armata* individuals grows on nearby Isla Angel de la Guarda in the Gulf of California (Moran 1978).

The largest populations of *B. armata* in the State of Baja California grow on granitic rocks that receive water from springs and seeps draining from adjoining volcanic caprock, notably Arroyo Grande in the southern Sierra Juárez, Arroyo El Berrendo in the southern Sierra San Pedro Mártir, and the southern Sierra La Libertad (Fig. 1). Large concentrations of dwarf, upland populations of *B. armata* also occur on resistant, weakly fractured granitic rock units along portions of Arroyo El Berrendo (see also Franco-Vizcaíno et al. 2007), at Cataviña and southeastward to Misión Santa María, as well as the southern Sierra La Asamblea, and southern Sierra La Libertad. Many of these upland palms are <5 m tall and occur

in thousands of small discontinuous populations, either as single trees or clusters of <10 trees each in small catchment depressions, sediment-filled bedrock fractures and basins, as well as in sediments at the base of large bedrock slopes (Fig. 4–5).

The highest peaks of the southern Sierra San Francisco (ca. 1500 m, lat 27.6°N) contain lengthy riparian galleries of *B. brandegeei* along deep canyons carved into Pliocene basalt, the stream beds having intermittent exposed bedrock and secure surface water. Mountain palm oases, almost entirely *B. brandegeei*, occur sparingly over much of the Sierra La Giganta. Isolated colonies grow on the highest summits in the north (lat 26.9°N) as well as on Cerro La Giganta, 25 km NW of Loreto, where *W. robusta* is also found. Palm clusters occur along the crest of the range near the Gulf of California, centered at lat 25.7° and 24.8°N. *Brahea brandegeei* is most extensive in the heavy summer precipitation zone of the cape ranges, with sizable stands in the Sierra La Laguna and a small range east of La Paz (Fig. 1). Palms are broadly distributed along watercourses and slopes in association with thorn scrub below 1100 m, Mexican oak woodland from 1100 m to 1500 m, and Mexican pine-oak woodland above 1500 m. *Brahea brandegeei* is a widespread dominant on most major watercourses leaving the range, but palm galleries extend only intermittently into the surrounding alluvial plains.

Massive oases of *B. brandegeei* and *W. robusta* grow at the base of the mountains of the tropical southern peninsula (Fig. 1). In the Sierra La Giganta, these oases occur on broad washes at the interface between mountain volcanic units and Miocene sedimentary rock units near the coast. The palm oasis at San Ignacio is the largest single stand in the PRP. Many groves have *Phoenix dactylifera* L., the date palm of the Middle East, which was originally planted during mission times in the late 18th century (Nelson 1921; Aschmann 1959, 1997). In the cape region, large oases are found where primary watercourses encounter the coast. The coconut palm, *Cocos nucifera* L., occurs at several beach oases.

While introduced *P. dactylifera* is mostly found within the major agricultural oases of the PRP, this palm is locally naturalizing in *B. brandegeei* riparian oases in the mountains, including the Sierra La Libertad, the northern Sierra San Francisco near Misión Santa Gertrudis, on the southwestern flank of the range, and at numerous localities along the crest of the southern Sierra La Giganta (Table 1). It is also planted on ranches throughout the peninsula.

Our analysis of Google Earth imagery, field records, and low-altitude aerial surveys north of lat 27°N revealed significant range extensions for both *Washingtonia* spp. We found 66 populations of Washington fan palms, tentatively identified as *W. robusta*, in the Sierra La Asamblea (Table 1, Fig. 1–3), ca. 60 km ESE of the nearest recorded stands at Santa Inés and Misión Santa María. This range extension reduces the gap in *W. robusta* to the next stands south at San Ignacio to ca. 240 km. *Washingtonia* spp. were not found in either the Sierra La Libertad or the Sierra San Francisco. In addition, six juvenile *Washingtonia* individuals were recorded in the field near the terminus of Arroyo El Berrendo in the southern Sierra San Pedro Mártir, where *Washingtonia* has not been previously reported. The individuals were too young to identify to species. That these six juvenile individuals (< 2 m) could not be discerned in the imagery available at the time provides an example of how visual tallies on Google Earth can underestimate the size of populations. Depending on the classification, this discovery would extend the known distribution of *W. robusta* 75 km northwest from its previously known northern limit east of El Mármol (lat ca. 30°N), or the southern limit of *W. filifera* southward 90 km from its current limit in the southern Sierra Juárez (lat ca. 31.4°N).

North of Sierra San Pedro Mártir, palm oases are found on rain-shadowed, leeward sides of the peninsular ranges. One exception is a stand of *W. filifera* in the semiarid coastal Valle de Las Palmas, 50 km southeast of Tijuana (Orcutt 1883). We also discovered two small populations of *W. filifera* along a fault in the coastal rain-shadowed Valle Ojos Negros ca. 36 km ENE of Ensenada (Fig. 1). This is the first discovery of presumably natural populations of *W. filifera* in the coastal valleys of far northern Baja California since Orcutt's report more than a century ago.

DISCUSSION

In biogeography and ecology, it is important to develop baseline data to evaluate the dynamics of ecosystems over long time periods and broad spatial scales. An important achievement of Google Earth is the ability to map geographic data directly onto imagery. This eliminates several steps in the production of geographic data: (a) the original analysis of imagery independently of base maps, (b) the transfer of data from imagery to basemaps, and (c) the digitizing of basemap data into a geographic information system. The result is a speedier production of final maps and reduction of data loss in the transfer processes. The resolution of Digital Globe imagery also permits the identification of individual trees for classification, thus allowing estimation of density and cover. Regional change can be quantified from local scales, and variation in local patterns can be quantified with respect to the regional pattern. This is timely in view of recent concern for monitoring future biotic change in response to global climate change, but predictions can be rigorously constrained by empirical data. The detailed palm distributions presented here bring new insights on the regional ecology and biogeography of palms in the PRP. The inferences below can be treated as hypotheses for future research.

Temperature

Washingtonia and *Brahea* are frost-sensitive, but differences in the upper elevational limits suggest that *Washingtonia* spp. are more easily frost-damaged than *Brahea* spp. *Washingtonia filifera* can tolerate temperatures as low as −11°C, based on comparison of groves with nearest weather stations, and cold exposure trials (Cornett 1987). The northernmost oases at Twentynine Palms occur at the southern fringe of the Mojave Desert, a large elevated plateau with climate characterized by hard freezes from temperature inversions (Minnich 2007). We observed that throughout the PRP, *Washingtonia* spp. grow below 1000 m where ambient temperatures seldom drop below −5°C. *Brahea armata* in the southern Sierra San Pedro Mártir grows at elevations of 1400 m in association with chaparral and pinyon woodlands, with winter temperatures reaching −10°C, and with occasional winter snow cover. The highest summits of the Sierra La Laguna rise above the upper elevational limit of palms (1700 m) where freezing may limit their establishment.

Competition

The distribution of palms in the PRP may be influenced by competition from arboreal vegetation because both *Washingtonia* and *Brahea* are shade-intolerant. Growth of juvenile palms is suppressed by shade, but increases rapidly when stems are exposed to full sun through the removal of overstory by fire (Vogl and McHargue 1966). Palms are absent in Mediterranean climates north of lat 30°N, likely because stream courses are dominated by deeper-rooted riparian trees (mostly *Populus fremontii* S.Watson, *Platanus racemosa* Nutt., and *Salix* spp.) that have stronger resistance to floods than palms, which extract surface water (Cornett 1985*b*). In southern California, gaps in palm distribution occur on leeward eastern escarpments with dense riparian forests and include the northern San Jacinto Mountains, Laguna Mountain and Volcán Mountain, all with at least 40 cm average annual precipitation.

The sparseness of palm oases in dense thorn scrub of the Sierra San Francisco and the Sierra La Giganta in Baja California Sur may also be related to shade intolerance. Above 1200 m elevation, only local oases grow in dense oak woodlands, especially on north-facing slopes and along canyons. In the cape region, the co-occurrence of palms with thorn scrub and oak-pinyon woodlands in the Sierra La Laguna appears to be related to heavy summer precipitation. The seasonal persistence of soil saturation may permit the establishment and maturation of palms with associated thorn scrub and oak woodlands, even away from stream courses.

Fire

Palm oases commonly show evidence of natural and anthropogenic burning (Moran 1978), but it is doubtful whether periodic fire affects the distribution of fan palms. *Washingtonia* and *Brahea* are rarely killed by fire, typical of most members of the palm family. The shag of dead fronds along boles of *Washingtonia* and *Brahea* typically causes trees to burn up to the crown apices. Because their vegetative buds are well protected by living leaf bases, palms of both genera regrow after defoliation by fire (Vogl and McHargue 1966; Vogl 1968; Moran 1978). The removal of arboreal understory species permits the rapid growth of juvenile palms. In *W. filifera*, successive fires kill and remove outer vascular bundles of the bole, resulting in reduction in bole diameter and crown size. However, the consequential decline in transpiration improves tree survival during subsequent droughts (Vogl 1968). Charring increases trunk fire resistance. Long fire intervals limit selective pressures for recolonization.

The elevational limits of *B. armata* extend into the chaparral of the Sierras San Pedro Mártir, La Asamblea, and La Libertad, which burns at intervals of 50–100 years (Minnich and Chou 1997; Minnich et al. 2000). Palm oases in the desert, where fire may be rare even in millenial time scales, would have to be directly ignited by lightning or anthropogenic means (Vogl and McHargue 1966; Vogl 1968). Fire intervals in thorn scrub and Mexican oak woodland have not been documented, but the presence of few landscape fire scars on Google Earth imagery suggests that burning is even less frequent or severe than in chaparral. Moderate Resolution Imaging Spectroradiometer (MODIS) imagery bands for June (before monsoon rains) reveal no major burns in the PRP south of the Sierra San Pedro Mártir since the onset of the database in 2002, including productive thorn scrub and oak-pinyon woodlands of the Sierra La Laguna (MODIS Rapid Response System 2002).

Water Availability

Google Earth imagery reveals that palms are remarkably sparse or absent from most of the major watercourses in the Baja California peninsula, but are found with the greatest abundance in moister mountain watersheds above 1200 m. They are absent from most low mountain ranges that have insufficient fluvial or substrate water sources for viable colonization. Over most of the peninsula, imagery shows scoured streambeds of exposed bedrock and fresh unweathered sediment lacking vegetation, indicative of recent bank-full runoff. Small disjunct palm oases are widespread in smaller tributaries and at springs and seeps in the headwaters of catchments having lower stream volume but greater precipitation than the surrounding desert.

Dwarf colonies tend to occur in outcrops of large granite boulders (tors) where some runoff from impermeable rock surfaces can be stored (Fig. 4–5). These include bedrock fractures, local sediment-filled depressions that host temporary pools, and at the base of large bedrock slopes. These catchments have low infiltration but sufficiently frequent rains and bedrock runoff to maintain small units of permanently moist soils, leading to "bonsai" palms. Because of the sparse plant cover in such habitats, it seems reasonable that precipitation stored in fractured rock formations might provide sufficient moisture for a precarious existence. The abundance of tall palms in nearby primary arroyos suggests that dwarf palms represent phenotypic plasticity to local conditions rather than being genetically fixed ecotypes. The absence of palms in adjoining bedrock units, mostly volcanics, weak granites, or alluvium, strongly indicates that the survival of palms is coupled with the unique hydrology of these weathering-resistant intrusive rock units.

Washingtonia appears to have higher water requirements than *Brahea.* Where the two genera are together, *Washingtonia* occupies the wetter sites, with *Brahea* growing at the edge of oases or along drier watercourses (Fig. 2–3). Further research is required to demonstrate that drought tolerance can explain the more widespread distribution and higher elevational limits of *Brahea* spp. compared to *Washingtonia* spp.

Lithology and Substrate

Google Earth imagery revealed that palm distributions coincide with lithologic contacts in several areas. In the Sierra La Asamblea, palms are abundant in granitic rocks but avoid pre-batholithic and Tertiary volcanic exposures. In the southern Sierra San Pedro Mártir, palms are absent from volcanic upper mesas and arroyos, but they become frequent in arroyos downcut into granitic basement. In these tablelands near Arroyos El Berrendo and Matomí, it appears that runoff from fractured granite boulders retained in inter-rock soils and along watercourses may provide sufficient water for palms, while water retention of volcanic caprock may be limited by high permeability. The overlying volcanic rocks might thereby become large sources of permanent water at the contact with the granite basement.

In the Sierra La Libertad, however, palms are scarce in fault-shattered granites, but are abundant in Pliocene volcanic caprocks overlying granites. Populations in the southern Sierra La Giganta grow almost exclusively on rapidly-eroding, white Miocene sedimentary rocks. Elsewhere in the Sierra La Giganta, the abundance of palms appears to be limited by the dominance of Tertiary extrusive rocks and broad aggrading washes with deep water tables.

Riparian Habitat and Flooding

The availability of supplemental water in oases presents a dilemma for palms, because they have both a high demand for water and shallow roots that can be easily detached by storm runoff. In the PRP, oases are periodically denuded by debris flows generated by runoff from North American monsoon thunderstorms, as well as from tropical cyclones (Fig. 6–7). It has been hypothesized that in steep escarpments runoff from winter storms, summer thundershowers, and tropical cyclones might uproot palms faster than they can re-establish by long-range seed dispersal (Minnich and Franco-Vizcaíno 1998). Colonization is accomplished by long-range dispersal of seeds in the digestive tracts of birds and mammals such as coyotes (Cornett 1985*a*,*b*), as well as by humans (Moran 1978; Hicks 1989). High erosion rates produce heavy loads of stream sediments with very large clasts (rock fragments) that tear out palms more efficiently than the sheer force of water alone. Palms are nearly absent from watersheds along precipitous fault escarpments with shattered bedrock and high erosion rates, including the Santa Rosa Mountains, the eastern escarpments of the Sierras San Pedro Mártir and La Libertad, and the northern Sierra La Asamblea.

Our observations revealed that dense oases have some capacity for local "self determination" by stabilizing fluvial sediment. Oases often exhibit a pollywog [tadpole]-shaped population distribution, with a dense head of stems upstream and a tail of progressively thinner populations downstream with increasing current (Fig. 8). Palms seem to colonize sites in a positive feedback process, with increasing palm stem densities entrapping more sediment, reducing the potential for floods to uproot them, which in turn facilitates sediment colonization.

In the field, we have also observed root systems of *B. armata* cemented by carbonates onto granitic bedrock, thus forming a hold-fast that protects individuals from being easily uprooted (Fig. 7). High carbon dioxide concentrations in the soil, due to root respiration, can combine with water to form carbonic acid. This appears to favor the dissolution of minerals such as feldspars and micas in granite, resulting in the formation of calcium carbonate that can cement to weathered rock.

The structure of stands suggests that palms partially control their destinies in a high-runoff environment. Trees at the upstream end trap sediment, which in turn supports the colonization and persistence of their down-slope neighbors. Mortality from storm runoff is dominant at the base of colonies, where uprooting develops with increasing stream volume. Many such stands grow in upper stream banks and stream terraces, above storm flow, downstream of rock barriers, at tributary junctions, and along oxbow bends in streams, all areas of diminished local stream flow and aggradation.

Palms seldom extend from mountain canyons into surrounding alluvial fans and plains likely because subsurface water rapidly drops below their rooting depth, but palms extend great distances toward the sea along arroyos with large watersheds or from highlands receiving high precipitation.

Long-Term Population Dynamics and Changes in Distribution

We hypothesize that the dynamics of palms over long time scales depend on their position in watersheds. Our observations revealed that palm oases in upper catchments are likely the foundation of the species because these areas support fixed populations on cliffs, streams, springs, and "vernal pools" that are safe from flooding. These populations are perpetual sources for seed dispersal to lower watersheds by fluvial processes and animal transport. Farther downstream, abundant gallery forests of palms along trunk streams experience large temporal variability in abundance, including periods of extirpation and re-colonization due to floods. Farther downstream are isolated strays, with the lowest stream courses near the ocean lacking palms altogether. Strays come and go in random distribution with successive floods. In the northern peninsula, the present distribution of palms along trunk streams may be less extensive than "normal" because of hurricane Nora in 1997, which made landfall on the Pacific Coast at lat 29.5°N as a Category 1 hurricane.

In the southern peninsula, isolated massive populations of palms occur in agricultural oases at the base of watersheds. Many occur in contact with coastal early Tertiary beds, volcanic bedrock barriers, and coastal estuaries.

Historical Analysis

The long-term dynamics of palms cannot, of course, be assessed from a static database of Google Earth imagery. However, some insight can be gleaned from historical sources. Palms have been recorded in the PRP since the initial Spanish colonization of the region in the 18th century, and were frequently highlighted because they were evidence of water. Such historical documents do not support the hypothesis of major change over the past three centuries (Burrus 1966; Minnich and Franco-Vizcaíno 1998; Brown 2001). The Biological Survey expedition of 1906 recorded palms in the same areas where they are seen presently (Nelson 1921). The northern limit of palms seen by Jesuit priest Wenceslaus Linck in 1766 on the eastern escarpment of the Sierra San Pedro Mártir is in the same canyon as today (Burrus 1966; Minnich and Franco-Vizcaíno 1998). Although the Spanish wrote during the Little Ice Age (ca. 1650–1850), there appears to have been little change in the distribution of palms over the period of modest global warming during the past three centuries. Plant migrations often lag behind climatic fluctuations, even at scales of millenia. In long-lived communities, a span of centuries is brief for even short-term population changes. Selection processes that result in changes in recruitment or disturbance patterns require several generations to reach mature phases of vegetation (Sauer 1988; Thompson 1988, 1990).

Anthropogenic Dispersal of Palms

Palms were deliberately introduced to many areas of the PRP, especially the exotic *P. dactylifera* (Aschmann 1959,

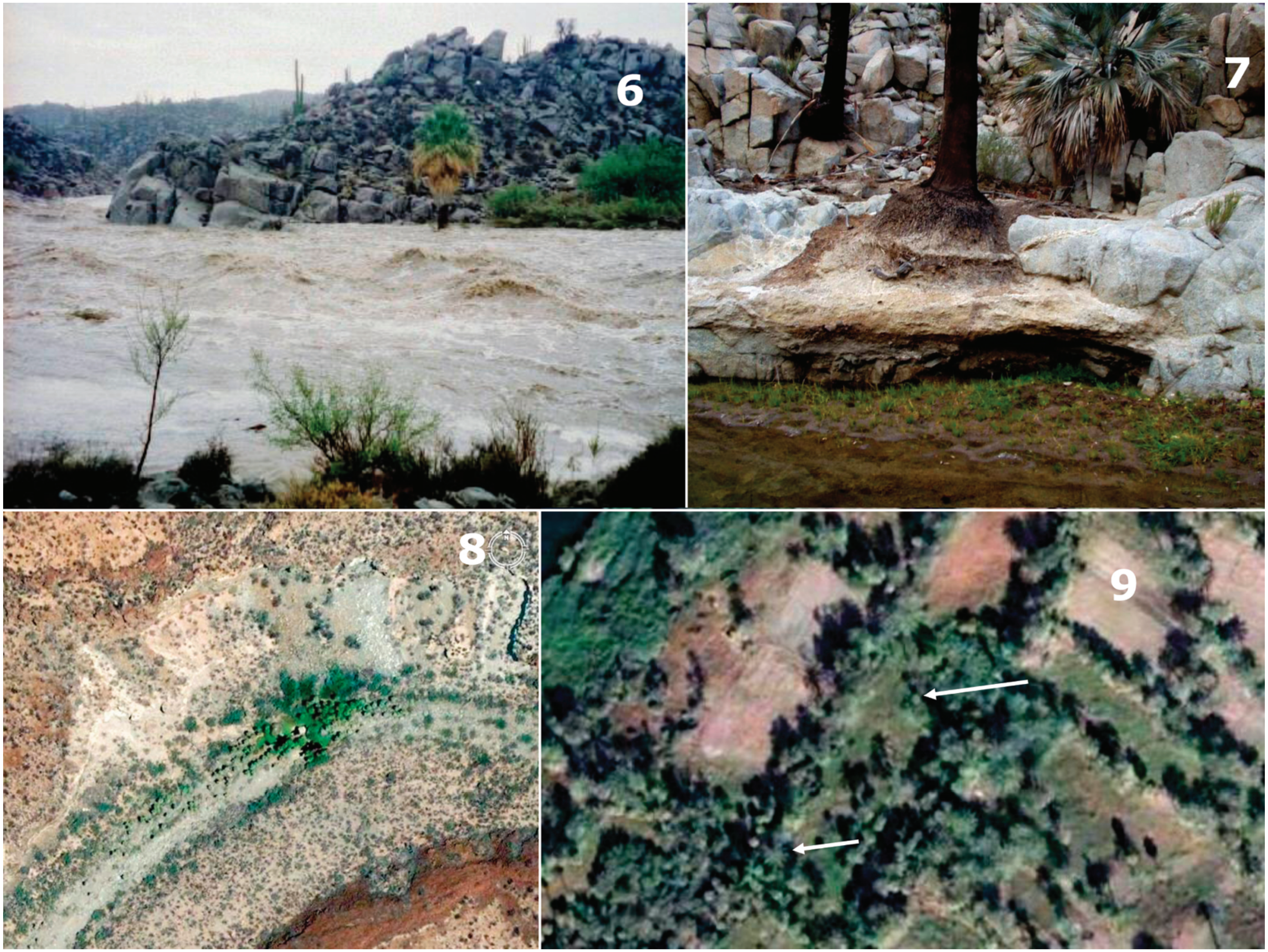

Fig. 6–9. Fan palm oases in the Baja California peninsula (Mexico).—6. Flooding due to Tropical Storm Juliette at Cataviña on 3 Oct 2001 (digitized from photo by MSC).—7. Roots of *Brahea armata* exposed by debris flow, showing holdfast of soil carbonates cemented to granitic bedrock, at Arroyo Matomí in the southern Sierra San Pedro Mártir (photo by EFV).—8. Google Earth image of a "pollywog" oasis in the northern Sierra La Giganta with a dense "head" of *Brahea brandegeei* upstream on the right thinning to a "tail" of open palms downstream to the left.—9. Google Earth image of *Phoenix dactylifera* (large fronds, short arrow) and *Brahea brandegeei* (small blue crowns, long arrow) in a cultivated landscape at San José de Comondú, Baja California Sur.

1997). Some plantings appear to have contributed to local range expansions of native palms. For example, palms are rare in the northern Sierra San Francisco, the primary population comprising *P. dactylifera* and *B. armata* at Misión Santa Gertrudis (Fig. 1, Table 1). The palms in the mission grounds are planted, many in rows, and it is suspected that rare *B. armata* in nearby drainages are not native but volunteered by long-range seed transport from plantings at the mission (Aschmann 1959, 1997). And although *W. filifera* occurs in southern Nevada (Cornett 1988), the status of these populations is ambiguous due to the historical removal of fan palms by early settlers and subsequent ornamental planting and naturalization (see e.g., Turner et al. 1995: 403).

The distributional patterns of palms in the PRP suggest that human transport spread *W. robusta* to many areas of the peninsula prior to European contact. Jesuit missionaries made clear that *W. robusta* was a favored ethnobotanical plant among aboriginal peoples. During his 1766 expedition to the Sierra San Pedro Mártir from Misión San Borja, Linck wrote that ''two kinds of palm trees can be distinguished: one, ashen-colored and not very useful [*Brahea* spp.]…; the others, green-colored, tall, and useful for various purposes…'' (Burrus 1966). The nutritional value of *Washingtonia* fruits rivals that of *P. dactylifera* (Cornett 1985*a*). Hence, human transport would have been more likely for *Washingtonia* spp. than *Brahea* spp. Rapid dispersal is consistent with findings of unexpectedly low genetic differentiation between isolated populations of *W. filifera* (McClenaghan and Beauchamp 1986), likely due to transport by coyotes or birds, both of which eat the fruit, as well as by aboriginals (Hicks 1989).

Google Earth imagery shows that *Brahea* spp. are widespread in remote mountains of the entire peninsula and are the only native palms present in the Sierras La Libertad and San Francisco, and most of the Sierra La Giganta. In the cape region, *B. brandegeei* is the only palm in the Sierra La Laguna and other nearby ranges. However, the only ''natural'' populations of *W. robusta* in the southern peninsula appear to occur on Cerro Loreto and on the eastern escarpment of the Sierra La Giganta near lat 24.8°N, but these have not been confirmed by botanical collections.

Most *W. robusta* in Baja California Sur, however, are found in massive oases with secure water, from San Ignacio southward to the cape region (Table 1), that were long settled by indigenous peoples (Arriaga et al. 1997; Maya et al. 1997). Such oases are thus cultural landscapes (Fig. 9) in which the natural versus anthropogenic origin of palms cannot be distinguished. This has likely contributed to the widespread belief that the center of *W. robusta* distribution is in the tropical southern peninsula (Wiggins 1980; Henderson et al. 1995; Felger and Joyal 1999; Felger et al. 2001). We propose that indigenous peoples may have dispersed *W. robusta* to the large settled oases in the southern peninsula prior to European contact, and that its center of genetic diversity may, instead, be found in the widespread populations distant from settlements that occur in the Central Desert from El Mármol through Cataviña and Misión Santa María to the Sierra La Asamblea (Fig. 1–3). This finding may have important implications because information regarding the locations of the original collections of the type specimens of both *Washingtonia* spp. is lost or confusing (Ishihata and Murata 1971), and the taxonomy of the genus requires a modern re-examination (Wiggins 1980; Henderson et al. 1995; Felger and Joyal 1999; Felger et al. 2001).

CONCLUSIONS

The first map of palm oases presented here brings fresh insights that will lead to new investigations on the regional ecology and biogeography of *Washingtonia* and *Brahea* fan palms in the PRP. Fan palms occur in areas of supplemental water in semiarid mountains. They are intolerant of shade and their distribution seems to be limited by competition from deep-rooted trees in the higher-precipitation regions of both the southern and northern PRP. The continuity of palm populations is not secured by the largest stands along watercourses, but rather by small populations in small catchments with reliable surface water that are least affected by floods. Palms are shallow-rooted and can be removed by debris flows generated by thunderstorms and hurricanes, but may partially ''control'' their destinies by advancing upstream in a positive feedback between sediment entrapment and colonization of sediment. They are absent from semiarid fault escarpments subject to high erosion rates. Numerous upland populations of dwarf *B. armata* grow in small watersheds on granite bedrock slopes. *Washingtonia* spp. appear to be less tolerant of freezing temperatures and to have higher water requirements than *Brahea* spp. The occurrence of widely separated palm populations throughout the PRP supports the hypothesis that isolated wet sites are readily colonized by long-range dispersal over long time scales. Historical evidence indicates that palm distributions have been stable during the past three centuries. That *W. robusta* in the tropical southern peninsula is mostly confined to large agricultural oases suggests it may have been dispersed there by indigenous peoples before European contact.

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